

TREE SPECIES USED BY BIRDS IN LOGGED AND UNLOGGED MIXED-CONIFEROUS FORESTS

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A number of studies have examined the possible ways birds use their habitat to permit optimum exploitation and to allow coexistence of different species. Habitat partitioning may occur if, for example, each species possesses a characteristic foraging height distribution (Hartley 1953, Morse 1968, Diamond 1973). Birds may also divide the vegetation into various horizontal levels (Colquhoun and Morley 1943, MacArthur 1964, Balda 1969). Individuals of a given species may also primarily restrict their activities to specified zones in the tree such as the trunk or outer branches (Hartley 1953, MacArthur 1958, Morse 1967a, 1967b, Stallcup 1968, Sturman 1968, Koch et al. 1970). There is evidence that some avian species do have preferences for certain plant species (Hartley 1953, Morse 1967b, Balda 1969, Willson 1970, Jackson 1970, Austin and Smith 1972). These factors by acting individually or in concert may interact to produce habitat partitioning for the various avian species in the community.

It has been suggested that plant species diversity has little effect on a community's bird species diversity which instead, is dependent upon foliage height diversity, at least in homogeneous environments (MacArthur and MacArthur 1961). It is the vegetation profile which determines bird species diversity and not the number of plant species present. Yet, the nature of the vegetation may be important in a heterogeneous environment. MacArthur (1964) found that in the complex environment of the Chiricahua Mountains, Arizona, birds "apparently used more than just profile in selecting suitable habitats; presumably the addition of nest holes and water, the change from oak to pine and from sparse to dense foliage, all made significant changes in the acceptability of the habitat for many species." It appears that birds do not regard all trees of the same height and profile, belonging to different species, as being equally desirable for activities such as foraging and nesting.

The purpose of this investigation was to determine if birds select certain tree species in a mixed-coniferous forest, and if so, to what extent the use of a logged area differs from that of a virgin forest. Results from this study may suggest some guidelines for future timber harvesting practices in the Southwest.

STUDY AREA AND METHODS

Study area.—The study site was located on the Willow Creek watershed (202 ha logged; 131 ha unlogged), approximately 80 km south of Springerville on the Apache-Sitgreaves

National Forest, Greenlee Co., White Mountains, Arizona. It is a U.S. Forest Service experimental watershed ranging in elevation from 2682 to 2804 m.

Vegetation.—Sampling of trees with dbh (diameter at breast height) ≥ 7.6 cm in the unlogged and lumbered areas was conducted using the plotless point-quarter method (Cottam and Curtis 1956). One-hundred stations (400 trees) were sampled in a 15.5 ha study plot in each area. For the tree in each quadrat closest to the center stake, the following data were taken: tree species; tree height; dbh; and distance from the center of the trunk to the stake. Quaking aspen (*Populus tremuloides*) and snags (dead trees) had not been removed when part of the watershed was logged in the summer of 1972.

Foliage volume.—Use of the available live foliage volume was analyzed by estimating the amount of foliage for each tree species in the modified and unaltered habitats. Data for these analyses were collected simultaneously with those of the point-quarter measurements. Tree species, tree height, height to the first live branch, length of the longest branch, and distance from the center of the trunk to the first live foliage on the longest branch were recorded for each tree sampled.

An estimate of live foliage present for a given tree species was determined by calculating the total amount of foliage for each tree and then subtracting from this the value of the dead volume (the inner area of the tree which was devoid of live needles or leaves). To obtain volume in terms of m^3/ha for a particular tree species, I divided the live volume for each species by the number of trees of the given species sampled. Next, I multiplied this by the absolute density of the species sampled. The result is live foliage volume (m^3/ha) of the given tree species.

The actual formulae used to estimate volumes for a given tree were:

Live foliage volume for spruces (*Picea* spp.), firs (*Abies* spp.), and Douglas-fir (*Pseudotsuga menziesii*) = $\pi/3 (r_0^2 h_0 - r_1^2 h_1)$ where $h_1 = h_0 - (r_0 - r_1)$

Live foliage volume for pines (*Pinus* spp.) = $\pi (r_0^2 h_0 - r_1^2 h_1)$ where $h_1 = h_0 - (r_0 - r_1)$

Live foliage volume for quaking aspen = $4/3 \pi (r_0^3 - r_1^3)$

In all cases, r_0 represents the length of the longest branch and r_1 is the distance from the center of the trunk to the beginning of the live vegetation on the longest branch. h_0 represents the height of the tree's live vegetation (i.e., total tree height—height to first branch). h_1 is the height of the portion of the tree containing branches which have dead foliage, minus the height to the first branch.

Avian tree species selection.—When a bird was observed in a tree, the following data were recorded: bird species, tree species, and activity (singing, foraging, observing, or resting). Data were collected at all daylight hours throughout the summers of 1973 and 1974 by systematically traversing the study plots along established parallel transect lines. One observation per bird was recorded and the number of such observations is indicated by N. I obtained 4868 total observations in the unharvested site and 4964 in the modified habitat.

Preferences for certain tree species were noted by comparing frequency of use of a particular tree species with its percent availability in the habitat as calculated from foliage volume data. Relative density of snags as determined from point-quarter data was used for comparative purposes as no foliage was found on them.

Data were analyzed separately for the Yellow-bellied Sapsucker (*Sphyrapicus varius*), Mountain Chickadee (*Parus gambeli*), Ruby-crowned Kinglet (*Regulus calendula*), Yellow-rumped Warbler (*Dendroica coronata*), and Gray-headed Junco (*Junco caniceps*). These 5 species were selected because they are representative of hole, open-cup, and ground nesting species and because they were present in sufficient densities in both

habitats to afford adequate sample sizes. Data for the entire avifauna included these as well as all other species. Niche breadth was calculated for each species using the following formula (Shannon 1948): $B = -\sum p_i \ln p_i$ where B is the habitat niche breadth and p_i is the proportion of observations occurring in the i^{th} tree species.

Avian densities.—Species densities were determined using the spot-map method (Williams 1936) whereby a 15.5 ha grid pattern was established in the unlogged and harvested areas using plastic flagging placed at 25 m intervals along 9 parallel lines, each 390 m in length, and 50 m apart. I labelled each flag with a number corresponding to the transect line and a letter corresponding to the distance traveled from the beginning of the line. Censusing was conducted 6 times per month (June, July, and August) in each habitat.

RESULTS

Vegetation.—In the unharvested area total tree density was 626.2 trees per ha versus 167.7 in the harvested site (Table 1). In both habitats, Douglas-fir had the highest density as well as the highest importance value. In the logged area snags and quaking aspen, neither of which were removed during logging, were of considerable importance. The category "snags" contained representatives of every tree species.

Foliage volume.—Ponderosa pine (*Pinus ponderosa*) (35.9%), followed closely by southwestern white pine (*Pinus strobiformis*) (35.3%), and Douglas-fir (17.6%) had the greatest foliage volume in the unharvested site (Table 1). However, in the logged habitat quaking aspen contained the majority of total foliage volume available (53.1%). Southwestern white pine (12.6%) and Douglas-fir (11.0%) comprised considerably less foliage volume than did aspen.

Avian tree species selection.—I used Neyman's (1949) statistical test to evaluate differences between actual avian tree species use and the expected number of observations based upon the foliage volume availability of the various tree species. The following results were all statistically significant at the $P \leq 0.05$ level unless otherwise indicated.

Tree species preferences for the entire avifauna in the unaltered site (Fig. 1) indicated significant preferences for Douglas-fir, white fir (*Abies concolor*), and Engelmann spruce (*Picea engelmanni*). However, certain tree types were not used to the extent to which they were available such as ponderosa pine, southwestern white pine, and snags. There was no significant difference between the volume of aspen available and bird use either by the total avifauna or by the 5 individual avian species in the unlogged habitat.

In the lumbered area, avian use of aspen was significantly less than expected based on the volume of foliage present for both the total avifauna and the 5 selected bird species. Douglas-fir and Engelmann spruce were strongly

TABLE 1
TREE SPECIES DENSITY, IMPORTANCE VALUE, AND FOLIAGE VOLUME

Unlogged area				
Tree species	Tree density (#/ha)	Importance value*	Foliage volume	
			(m ³ /ha)	Percent
Ponderosa pine	112.7	67.8	40910.4	35.9
Southwestern white pine	109.6	46.7	40253.3	35.3
Alpine fir	3.1	1.5	181.7	0.2
Douglas-fir	194.1	92.3	20000.5	17.6
White fir	51.7	24.5	4305.5	3.8
Blue spruce	12.5	5.2	552.6	0.5
Englemann spruce	31.3	13.0	2213.3	2.0
Quaking aspen	50.1	20.3	5565.9	5.0
Snag (dead tree)	61.1	28.7	—	—
Total	626.2	300.0	113984.1	100.0
Logged area				
Tree species	Tree density (#/ha)	Importance value*	Foliage volume	
			(m ³ /ha)	Percent
Ponderosa pine	4.6	16.3	1069.2	7.0
Southwestern white pine	8.8	14.5	1921.8	12.6
Alpine fir	13.0	20.8	497.0	3.3
Douglas-fir	42.3	64.0	1679.2	11.0
White fir	19.7	30.5	544.9	3.6
Blue spruce	9.6	13.9	421.0	2.8
Engelmann spruce	19.3	31.0	1030.1	6.8
Quaking aspen	29.3	51.2	8105.6	53.1
Snag (dead tree)	21.0	57.8	—	—
Total	167.7	300.0	15269.9	100.2

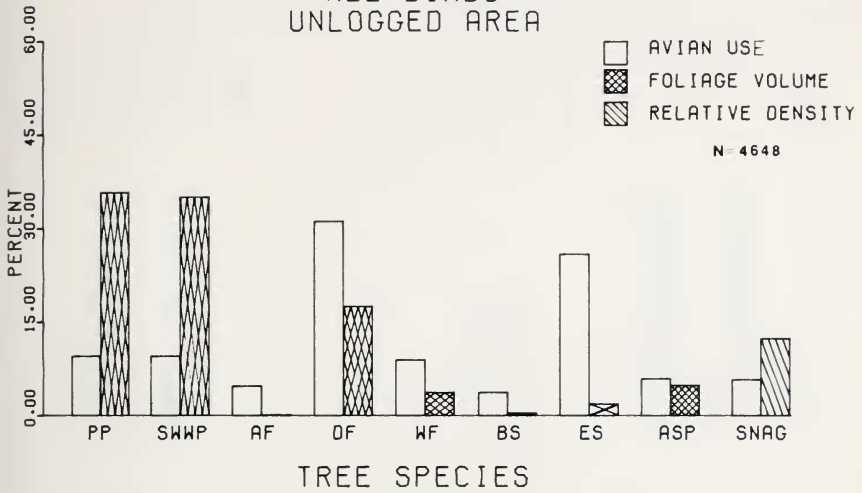
* Importance value is the sum of relative density, relative dominance, and relative frequency.

preferred, whereas ponderosa pine, southwestern white pine, and aspen were seldom used.

In both habitats the 5 avian species preferred spruces and firs and used the pines, aspen, and snags less than expected (Figs. 2-6). There were several exceptions to these generalizations. For example, Yellow-bellied Sapsuckers (Fig. 2) frequently foraged on snags in both habitats. No significant difference between use and availability was found for Douglas-fir or white fir in the unlogged site or for blue spruce and Engelmann spruce in the logged site.

It may be argued that since Yellow-bellied Sapsuckers confine most of their activities to tree trunks, a comparison of sapsucker use to tree species density

TREE SPECIES PREFERENCES
ALL BIRDS
UNLOGGED AREA



TREE SPECIES PREFERENCES
ALL BIRDS
LOGGED AREA

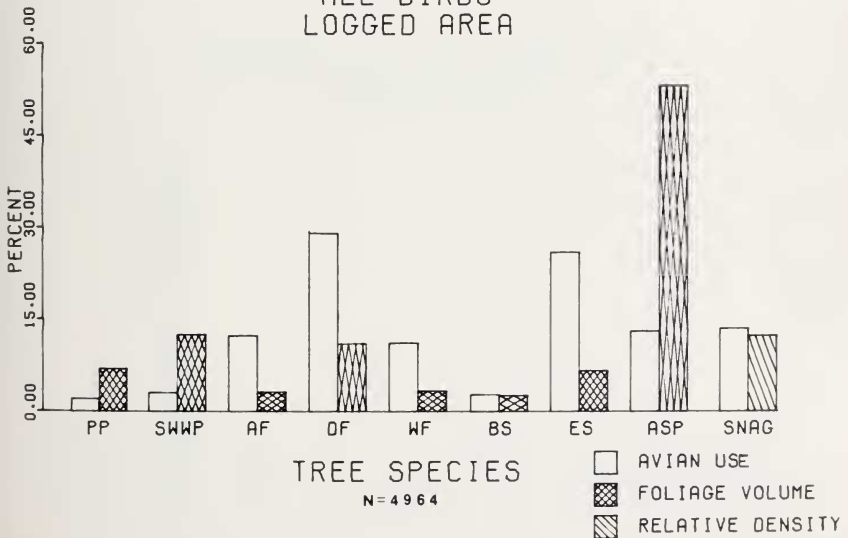


FIG. 1. Tree species preferences of all birds in the unlogged and logged areas. Plain bar is % of avian use. Crosshatched bar is % of foliage volume for the given tree species. Hatched bar is relative density of snags. Tree species were abbreviated as follows: PP—ponderosa pine; SWWP—southwestern white pine; AF—alpine fir; DF—Douglas-fir; WF—white fir; BS—blue spruce; ES—Englemann spruce; and ASP—quaking aspen.

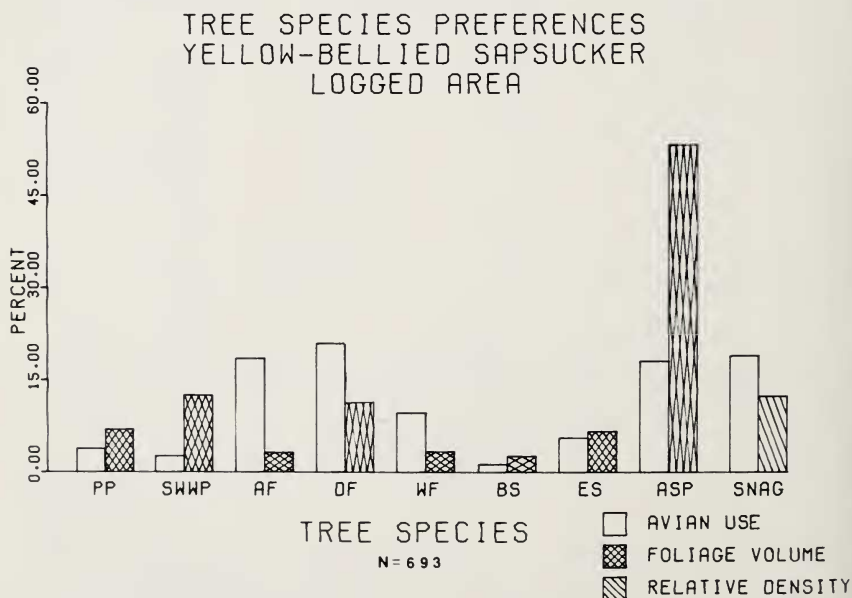
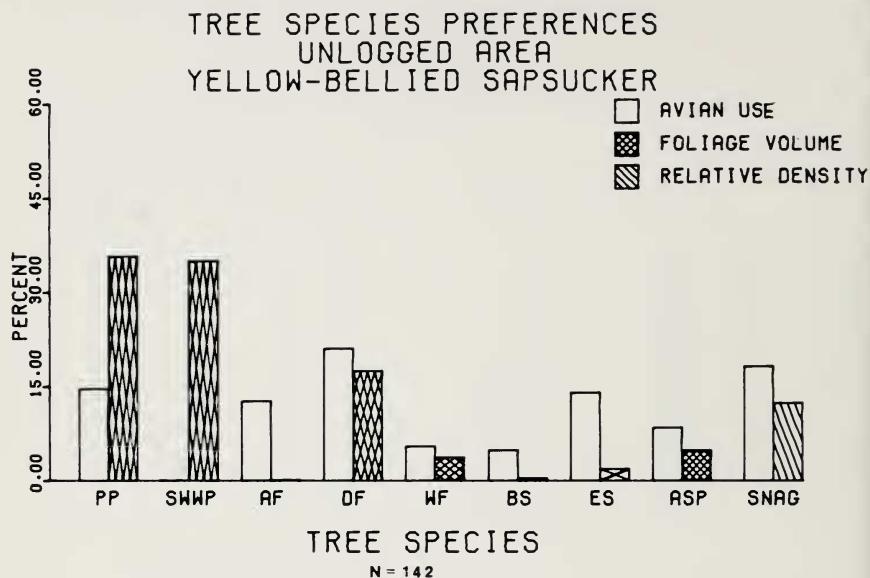
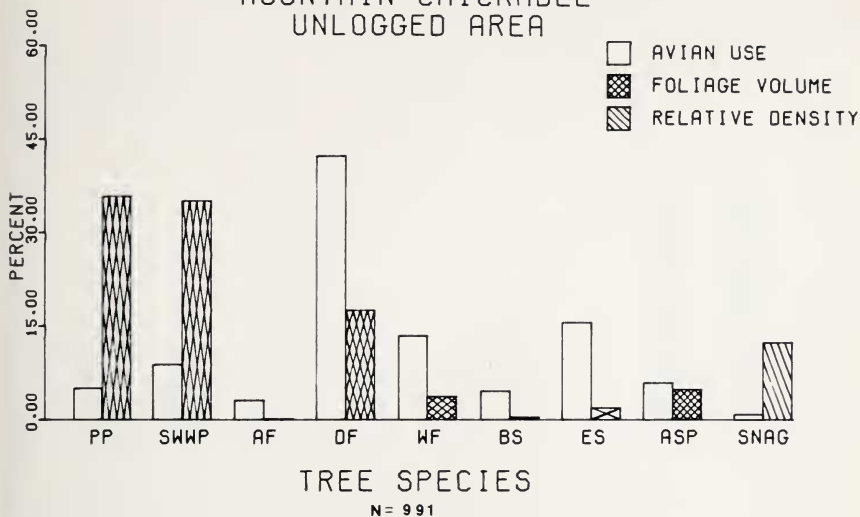


FIG. 2. Tree species preferences of the Yellow-bellied Sapsucker in the unlogged and logged areas.

TREE SPECIES PREFERENCES
MOUNTAIN CHICKADEE
UNLOGGED AREA



TREE SPECIES PREFERENCES
MOUNTAIN CHICKADEE
LOGGED AREA

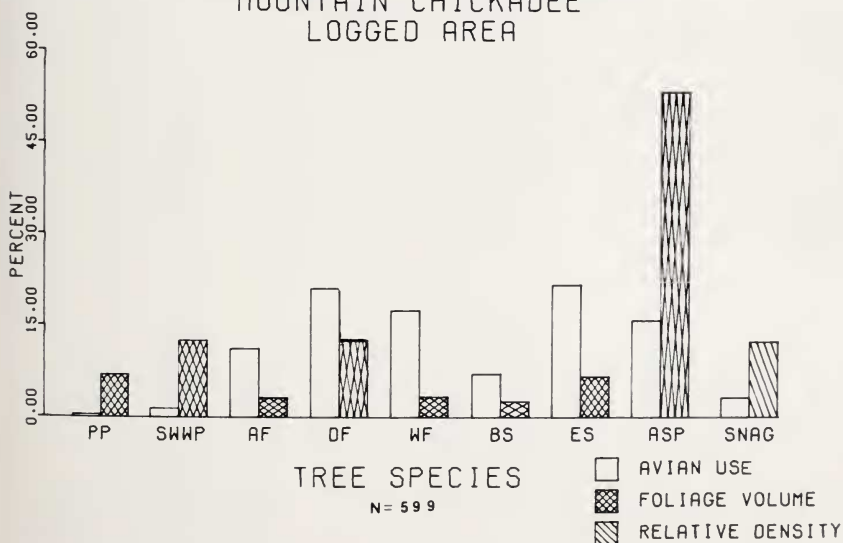
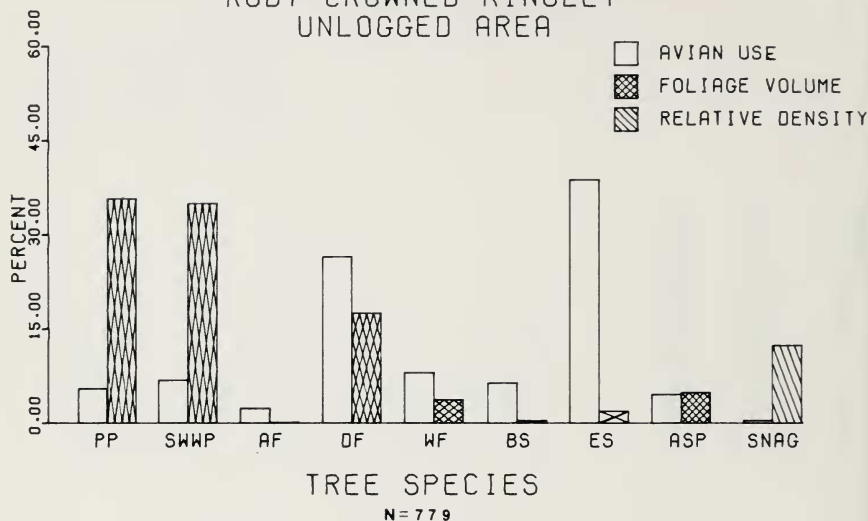


FIG. 3. Tree species preferences of the Mountain Chickadee in the unlogged and logged areas.

TREE SPECIES PREFERENCES
RUBY-CROWNED KINGLET
UNLOGGED AREA



TREE SPECIES PREFERENCES
RUBY-CROWNED KINGLET
LOGGED AREA

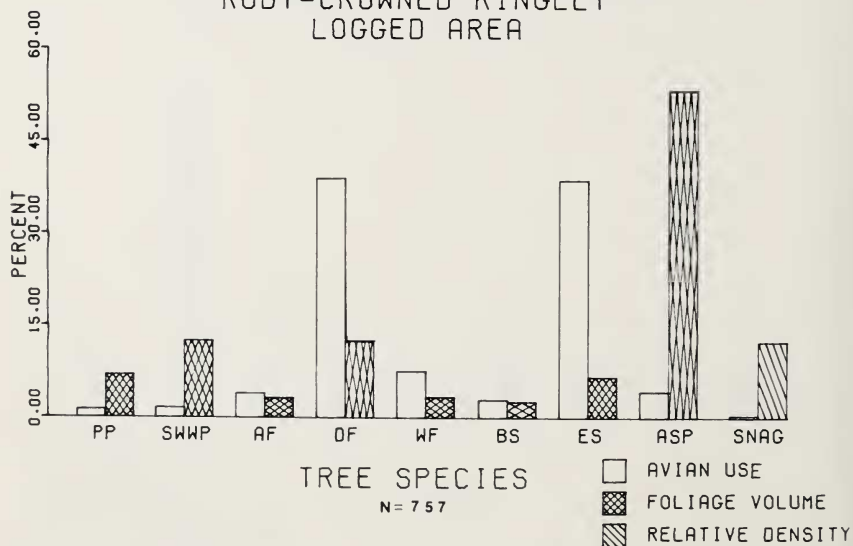
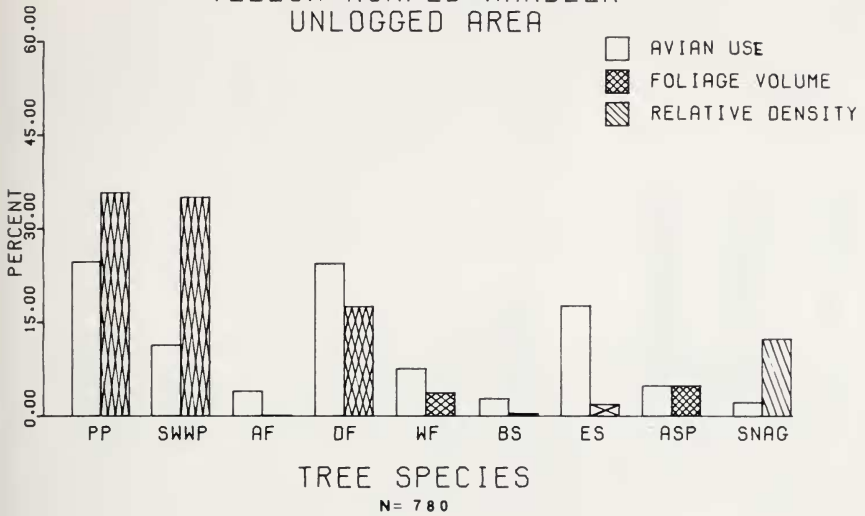


FIG. 4. Tree species preferences of the Ruby-crowned Kinglet in the unlogged and logged areas.

TREE SPECIES PREFERENCES
YELLOW-RUMPED WARBLER
UNLOGGED AREA



TREE SPECIES PREFERENCES
YELLOW-RUMPED WARBLER
LOGGED AREA

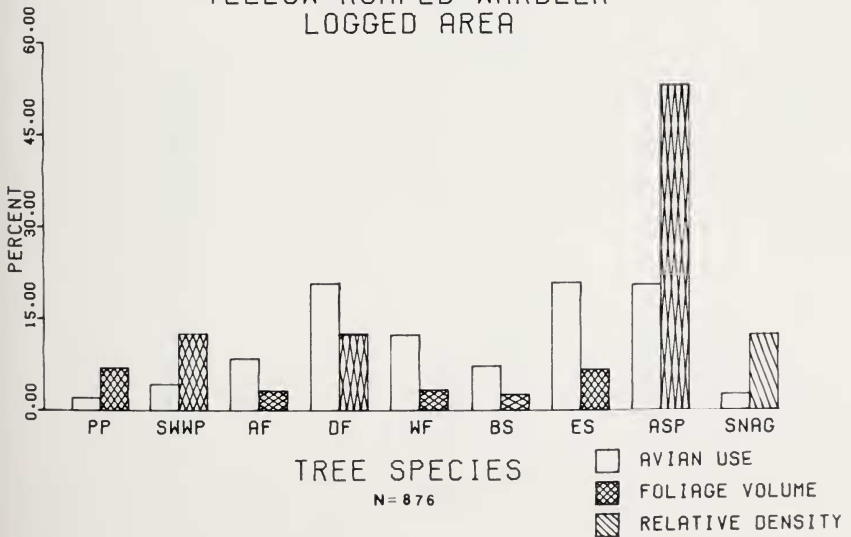


FIG. 5. Tree species preferences of the Yellow-rumped Warbler in the unlogged and logged areas.

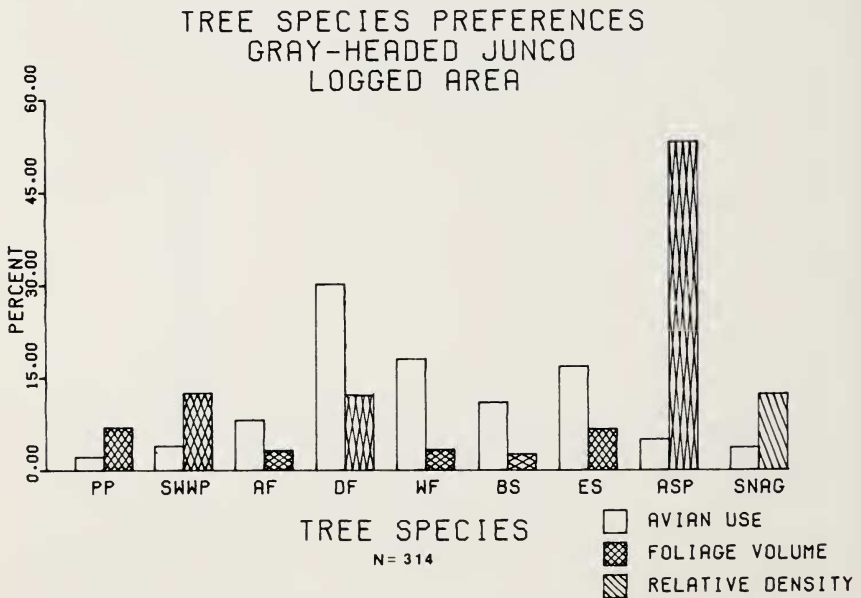
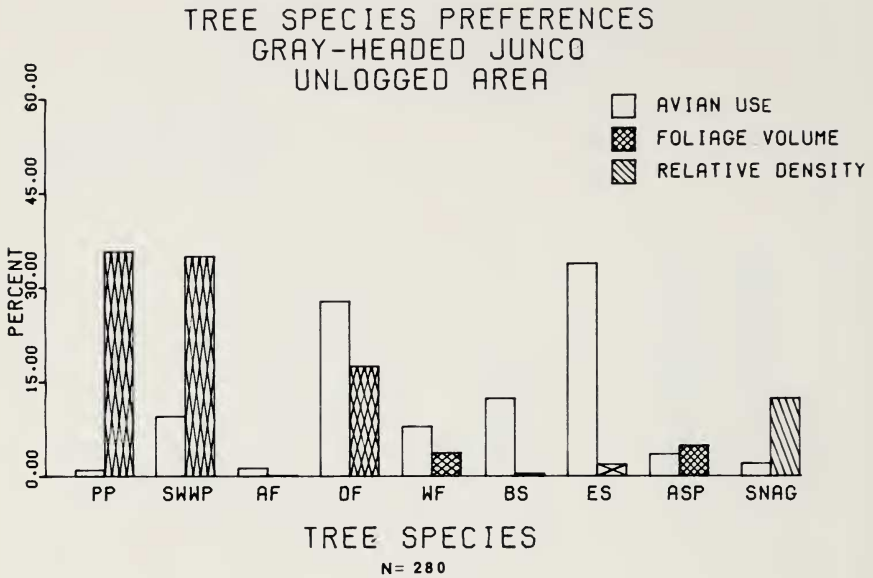


FIG. 6. Tree species preferences of the Gray-headed Junco in the unlogged and logged areas.

TABLE 2
NICHE BREADTH BASED ON TREE SPECIES USE

Bird species	Unlogged	Logged
Yellow-bellied Sapsucker	2.00	1.93
Mountain Chickadee	1.74	1.90
Ruby-crowned Kinglet	1.71	1.46
Yellow-rumped Warbler	1.91	1.96
Gray-headed Junco	1.72	1.90

* Niche breadth = $-\sum p_i \ln p_i$

might be more appropriate than a comparison to foliage volume data since presumably this species would be less dependent on the volume and type of foliage present than would be, for example, a foliage-gleaning species. However, the density of individual tree species is positively correlated with foliage volume per tree species ($r = +.69$ unlogged area, $r = +.41$ logged site). Results for the sapsucker were graphed in a consistent manner with the representation of the other 4 species and with the total avifauna.

For the Ruby-crowned Kinglet there was no significant difference between frequency of use and proportion of foliage volume present in alpine fir and blue spruce in the lumbered section (Fig. 4). The kinglet was rarely observed on snags.

The Yellow-rumped Warbler in the unharvested area (Fig. 5) visited ponderosa pine and southwestern white pine more frequently than did the other 4 avian species examined in detail. In the modified site, aspen was also frequently used, but far less than expected on the basis of tree availability.

Gray-headed Juncos in the unaltered habitat used alpine fir and aspen in proportion to their availability (Fig. 6). Tree use in the harvested area could not be associated with tree availability.

The Ruby-crowned Kinglet had a higher niche breadth value (Table 2) in the unlogged area than in the modified site. In contrast, the Mountain Chickadee and Gray-headed Junco showed higher values in the logged area. Niche breadths for both the Yellow-bellied Sapsucker and Yellow-rumped Warbler were similar in the modified and virgin forests. For the unaltered habitat, the Yellow-bellied Sapsucker ($B = 2.00$) had the highest niche breadth value followed by the Yellow-rumped Warbler ($B = 1.91$). These 2 species also had the highest values for the modified area, $B = 1.93$ and $B = 1.96$, respectively.

Although the Mountain Chickadee and Ruby-crowned Kinglet displayed strong preferences for the same tree species there were differences in terms of proportion of use. In the unmodified site the Mountain Chickadee used

TABLE 3

BIRD DENSITIES IN LOGGED AND UNLOGGED MIXED-CONIFEROUS FORESTS (#/40 HA)

Bird species	1974		1973	
	Logged	Unlogged	Logged	Unlogged
Yellow-bellied Sapsucker	15.8	10.6	20.5	10.2
Mountain Chickadee	11.8	44.7	30.8	58.9
Ruby-crowned Kinglet	42.1	71.0	23.1	74.4
Yellow-rumped Warbler	100.0	131.6	76.9	89.8
Gray-headed Junco	76.3	31.6	74.4	51.3
Total avifauna	544.0	632.9	758.0	865.9

Douglas-fir 40.9% and Engelmann spruce 13.6% of the time. However, the Ruby-crowned Kinglet frequented Engelmann spruce 45.8% and Douglas-fir only 22.7% of the time. A slightly different situation occurred in the logged site where the Mountain Chickadee was less specialized in its tree species use, selecting Douglas-fir and Engelmann spruce a total of 48.1%, whereas the Ruby-crowned Kinglet relied heavily on these 2 tree species (82.6% of its total foraging observations).

Avian densities.—The unmodified habitat supported a considerably larger avian community (Table 3) than did the logged site during the breeding season of each year. The Mountain Chickadee, Ruby-crowned Kinglet, and Yellow-rumped Warbler were more numerous in the virgin forest than in the lumbered site. Gray-headed Juncos were much commoner and Yellow-bellied Sapsuckers were slightly more numerous in the harvested site than in the unlogged area.

DISCUSSION

There are various possible explanations for avian selection of certain tree species while not using others. Factors affecting tree selection include food abundance, availability, and quality. Foliage may be important for birds in that it protects them from predators and inclement weather conditions and shelters the nest sites of numerous species.

In examining foraging behavior of English titmice (*Parus* spp.) Hartley (1953) found that although every tree species was used, some were far more intensively used. Tree species selection, in addition to height distribution and the tendency to search for food in different parts of the trees, permitted 5 species of titmice to occupy the same habitat. During periods of superabundant food supply, the ecological distinctiveness in feeding behavior disappeared among the 5 congeners, indicating the importance of competition for

food in determining foraging behavior (Hartley 1953). Studies by Palmgren (1930), Kluijver (1951), Gibb (1954), and Jackson (1970) also noted avian selection of certain tree species. However, Brewer (1963) stated that the Black-capped (*Parus atricapillus*) and Carolina chickadees (*P. carolinensis*) appeared to use the vegetation in relation to its abundance in the habitat in Illinois. Perhaps no habitat partitioning was evident in these species because they are primarily allopatric; moreover, Brewer suggests that competitive interactions may be a factor in producing this allopatry. Habitat partitioning achieved, in part, by tree species selection in Willow Creek was probably of more importance to some species than to others. No 2 species had exactly the same tree species preferences. Some potential competitors such as the Mountain Chickadee and Ruby-crowned Kinglet spent different proportions of their time in the same tree species. In the absence of data on abundance and locations of the food supply, it is not possible to state with certainty that competition for food was responsible for this habitat partitioning. In addition to tree species selection a variety of other possible mechanisms such as within-tree location preferences (Franzreb 1976), tree height selection, and foraging behavior (Franzreb 1975) were involved in habitat segregation.

During the nesting season the majority of birds in Willow Creek are insectivorous. The availability and type of food source may influence which trees birds prefer. Southwood (1961) found that the number of insect species associated with given tree species varied in Britain. Among genera of trees in his study (and which occurred in Willow Creek), poplars (*Populus*), pines (*Pinus*), spruces (*Picea*), and fir (*Abies*) had 97, 91, 137, and 15 insect species respectively. Overall insect abundances were not derived, hence, it was not known which tree species harbored the greatest densities of insects. Birds may select trees with only a few insect species if such prey items occur in sufficient numbers to make exploitation efficient. Insect abundance and number of species may also have varied among the tree species in Willow Creek.

The amount of vegetation present may influence insect numbers as evidenced by the number of foraging observations in heavy foliage. Successful foraging, however, is not solely dependent on the number of prey items per tree, but is more closely related to the density of insects (number per unit foliage volume). Search time required between successful captures, flying time between foraging sites, handling time per prey item, and the individual's degree of prey specificity may determine a bird's competency in exploiting a given resource. Those individuals selecting the portions of the habitat in which it is possible to achieve the highest degree of foraging success will have an advantage.

In the unlogged study area in Willow Creek, ponderosa pine and southwestern white pine, the tree species which contained the greatest amount of foliage volume were used far less than other tree species containing smaller amounts of foliage such as Douglas-fir and Engelmann spruce. Also, for the timber harvested area quaking aspen comprised 53% of the total available foliage and accounted for less than 15% of the total avian observations. However, foliage volume calculations were based on formulae which did not consider that pine and aspen leaves or needles are much less dense than those of spruces and firs. Therefore, the foliage per unit volume probably was much higher for the latter tree species than for the former. Hence, the disparity between avian use and calculated available foliage for some tree species may not be as great as shown.

Possibly the majority of birds infrequently visited pines and aspen because it was not energetically economical to use them. Perhaps search time was so prolonged that in all but the choicest sections of these trees, exploitation was impractical. Increased exposure to predators and inclement weather resulting from the openness of the vegetation may also have discouraged birds from using these species.

Snags harbor a variety of insects, many lying between the crevices on the bark or under the bark's surface, thus necessitating special morphological adaptations such as in the tongue or in the length and shape of the bill, to provide accessibility to prey. The many typically foliage-gleaning species in Willow Creek lack the necessary adaptations to extensively use snags but are adapted for exploiting live trees. Snags also harbor a different insect fauna than found in live trees (Anderson 1960). Difficulty in securing food as well as the type of insect prey available in snags, may have prevented or discouraged many birds, particularly foliage gleaners, from extensively using them.

Leaf morphology and size may influence the degree of avian use of a given tree species. The large leaf size of quaking aspen make it difficult for the majority of these birds, particularly the smaller passerines, to perch on an aspen branch or twig and reach the middle and outer portions of the leaves which may harbor insects. Hovering forms such as the Ruby-crowned Kinglet may encounter difficulty since aspen leaf movement occurs with even slight breezes. Further, aspens may not support similar insect densities and species found in coniferous trees.

Niche breadth values derived from tree species use data for individual bird species indicated differences existed between the unlogged and modified sites. In this context, I used the spatial model for the niche proposed by Hutchinson (1958) and expanded by Slobodkin (1962), Levins (1968), and MacArthur (1968). Avian niche breadth was considered as the degree of

diversity in tree species selection. It is the inverse of the degree of ecological specialization of a particular species within a given habitat (Levins 1968). Niche breadth does not indicate anything about tree species availability and is only suggestive of the evenness of tree species use for a particular bird species.

It is possible that very stereotyped species in the logged site which did not occur in sufficient numbers to be studied, were among the most affected by habitat modification. For example, logging in effect eliminated the Brown Creeper (*Certhia familiaris*), thus making it impossible to compare its foraging behavior in the 2 study areas. Perhaps those species present in sufficient numbers in both habitats to afford an adequate sample size, were the most plastic species, yet 1 of the 5 appeared to be fairly stereotyped in its foraging behavior (Ruby-crowned Kinglet). Stereotyped species should show a reduction in density and/or niche breadth in the modified site since they, presumably, restricted their activities to only the most useful tree species. This was true for the Ruby-crowned Kinglet. Such species may have enlarged territories in order to be assured of access to the minimum essential number of preferred trees. Thus, the number which the logged habitat could support would be reduced.

A more generalized species which maintained its density in the logged site map show a concomitant increase in niche breadth since it was possible to switch to normally infrequently visited tree species. A species might undergo a reduction in density in the modified site if either its niche breadth value was approximately the same in the 2 study sites (i.e., it could not become more generalized) or if the niche breadth value increased. The former situation was found for the Yellow-rumped Warbler and the latter for the Mountain Chickadee. Apparently the logged habitat was incapable of supporting as many Mountain Chickadees as the unmodified site. Perhaps this resulted from an insufficient amount of foliage volume of the favored tree species to fulfill all their requirements.

If a species, such as the Gray-headed Junco, achieves a higher density in the altered site than in the virgin forest, it may be fairly plastic and hence, exhibit an increase in niche breadth. Gray-headed Juncos were more numerous and had a higher niche breadth value in the logged than unlogged site. This junco, primarily a ground foraging species, is not as specific in its tree species selection as are foliage-gleaners. The Juncos also used slash (logging debris) which was abundant following lumbering. Slash provided an additional substrate which probably contributed to their higher density there.

Some species may have concentrated on the preferred tree species in order to acquire essential resources such as food, or perhaps it was a useful

strategy to further segregate the habitat among species in the logged site which may have been a more limited environment. Others may have become more generalized in order to take advantage of a larger portion of the habitat. Apparently avian species adjusted in various ways to the reduction in foliage volume and the reapportionment of the available foliage to different tree species in the harvested environment.

Future management decisions pertaining to timber harvesting should consider the heavy use of spruces and firs by birds. A decision to remove a substantial proportion of pines and aspen even though they are not frequently used by the avifauna, would adversely affect a number of species which rely upon these trees for nesting such as the Yellow-bellied Sapsucker and Warbling Vireo (*Vireo gilvus*) which nest in aspen, and for foraging such as the Grace's Warbler (*Dendroica graciae*) which forages in pines. I recommend that areas not be logged as heavily as Willow Creek which underwent a moderately-heavy overstory removal (removal of most of the trees forming the forest canopy). The majority of snags should not be harvested as they serve several significant functions such as providing nest sites for numerous cavity-nesting species.

SUMMARY

Variation in avian selection of tree species in a community which had undergone an overstory removal form of timber harvesting was compared to a virgin, mixed-coniferous forest, in the White Mountains, Arizona, during the summers of 1973 and 1974. Tree species preferences for all birds observed indicated Douglas-fir, white fir, and Engelmann spruce were the most frequently visited species in both habitats and were used in both the unmodified and logged areas in excess of the proportion of foliage volume they contained in the entire habitat. Ponderosa pine and southwestern white pine were frequented less than expected on the basis of availability. Although aspen constituted over 50% of the available foliage in the harvested habitat, birds did not appear to compensate for the reduction in density of firs and spruces by increasing their use of it. Whereas some species in the modified environment, such as the Mountain Chickadee, became more generalized and therefore less selective as to tree species, the Ruby-crowned Kinglet apparently became more restricted, and hence, more specialized in tree species preferences. Use of quaking aspen, the only species not removed during harvesting, and snags (dead trees) was higher in the modified than in the unaltered habitat.

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